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SOME OF THE FACTORS CONTROLLING THE MIGRATION AND SPAWNING OF THE ALASKA RED SALMON[1]

Henry B. Ward

University of Illinois

Man has always held the salmon in high esteem as a game fish and for the superior quality of its flesh for food. From the days when Roman Emperors reserved the salmon streams of Brittany for private use, and the wealth of Rome was spent lavishly to serve these fish at great banquets, an unbroken historic record awards to the Atlantic salmon the rank of chief among all fishes. Under the constant pressure of centuries its members have dwindled to a mere fraction of their former numbers, and today a few fish in the streams of northern North America and Europe represent the last remnant of the multitudes that swarmed in all the rivers from the Connecticut on the west to the Bay of Biscay on the east of the Atlantic.

The earliest voyagers along the Pacific shores of North America marveled at the vast hordes of salmon that there blocked the streams in their annual drive for the spawning grounds. Even today the greatly reduced and, alas, still rapidly diminishing numbers serve to maintain a commercial fishery that supplies the trade of the world and, measured by either quantity or value, ranks among the great industries of this continent. The conservation of such a resource rightly demands the careful consideration of scientific men while at the same time the striking life history of the Pacific salmon appeals most strongly to the scientific imagination as a biological problem of the highest interest.

The genus Onchorhynchus includes five species, collectively known as

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[1] This paper contains the substance of an address delivered before the Sigma Xi Chapter at the University of Chicago and at the installation of the Alumni Chapter of Sigma Xi at the Mayo Foundation. Presented before the Ecological Society of America at Chicago on December 28, 1920.

The paper is based on investigations made by the writer while in the service of the Bureau of Fisheries, and is published by permission of the Commissioner of Fisheries.

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the Pacific salmon and distinguished from their congeners of the Atlantic by structural features and also by biological peculiarities of a striking character. These species are commonly designated the Columbia River, the Silver, the Dog, the Humpback, and the Red or Sockeye salmon. All agree in the main features of their life history which stands in sharp contrast with the life cycle of the Atlantic salmon. In brief the story of the Pacific salmon is as follows: The full-grown fish make their appearance near the coast in the late spring or early summer, enter the inlets, push up the streams, somewhere in the headwaters find spawning grounds and there deposit eggs and milt. After completion of the reproductive function the adults perish. Resting on the gravels until spring the eggs hatch, the fry slowly descend the stream and disappear in the ocean. This story may be readily divided into three chapters, first the early life of the fish in fresh water, second the period of growth in the ocean, and third the fresh-water life of the adult terminated by reproduction and death.

It is the last period only which I wish to discuss in this paper and for clarity of treatment the account will be limited to the fresh-water period in the life of the adult sockeye salmon (*Oncorhynchus nerka*). Much that follows is equally true of the other species of Pacific salmon but is considered here solely in its relations to the sockeye. I propose further to limit the inquiry to that part of the migration which is found entirely in fresh water. It would be interesting to study the influences that lead the adult sockeye to desert its home in the sea, approach the shore, appear in shallow waters and enter certain estuaries. It is not enough to maintain that the approach of sexual maturity impels it to undertake this migration, for the explanation is at best partial. In regions like southeastern Alaska where the streams are numerous, and often several empty into the same estuary, the sockeye exercises a definite choice in entering some and passing by others. My studies have not been such as to justify consideration of this phase of the subject and accordingly it is passed with the mere mention. It is commonly held that the red salmon always choose a stream with a lake in or near which they spawn; but among the streams not utilized are those which carry lakes and apparently afford better opportunities for spawning than some that are visited.

The Journey to the Spawning Grounds

Once embarked upon a stream the sockeye moves steadily upwards. The definiteness of the migration route is well exemplified here also. To be sure there are some red salmon streams so simple that only a single path is offered; but in the majority of cases, no such compulsion exists. The options are numerous and from the human standpoint attractive, yet the sockeye follows a course that is not only fixed and exact but often bizarre and apparently erratic. This may be illustrated by the route of the migrating sockeye in the Skagit River (Washington). Having entered the river they follow the main stream past several tributaries of considerable size on either side until suddenly at Concrete they swerve sharply to the left, taking the channel of the Baker River and following that to Baker Lake where they spawn. Even more complex routes could be instanced. The salmon follow a precise course, the same one, as is shown by the practices of the fishermen and the traditions of the native tribes, that they have always followed.

A study of different localities readily shows that the route selected does not follow the larger volume of water, the clear or the turbid stream, the slower or the swifter current, the smooth or the rough water, the deep or the shallow stream, but passes indiscriminately from one to the other. The salmon persists in its definite course regardless of difficulties and obstacles. It seeks to rush the rapids in its way, and if beaten back by the force of the water returns again and again to the attack until its energy is exhausted; or if the water is low and passage impossible it waits until rains raise the water level and furnish it a path. It jumps continuously at the falls where swirling waters divert the leap, and is often dashed against the rocks so that, bruised and stunned, it floats down stream with the current, only to renew the attempt as soon as possible and repeat the effort until it meets success or death. Where natural or artificial barriers have been introduced into salmon streams the fish collect below them, striving constantly to surmount the obstacle until their energy is expended. In the early days of the salmon fishery when streams were fenced this habit made the fish an easy prey and the effacts of such methods may be recognized on fished-out streams in southeastern Alaska. In view of all this evidence it is certainly unwise to accept as normal the few isolated instances purporting to show that tagged fish have deserted one stream and have returned to salt water to seek another many miles away.

The definiteness of the migration route and the precision with which it is followed by the fish has impressed persons of all sorts who have been brought in intimate contact with the problem. The fishermen have given expression to their views in the parent stream theory. According to this hypothesis the adult fish returns to the very gravel in which it was hatched; the route traversed by the fry in seeking the ocean is followed in reverse order by the same fish when it returns to close its life history by the reproductive act. This view was very positively rejected by Jordan and others when first advanced; and indeed had to be, for the form in which it was phrased attributed the action to memory and held that the fish was able to follow so precise a course because it recalled the route it had followed in its way to the sea. It seems impossible to state the case in any way that conditions the behavior of the adult on the experience of the young and yet bring the statement into agreement with the viewpoint of science and the results of experiment. There is, however, a mass of fact which cannot be disregarded and for which a reasonable explanation must be found. This view, which forced itself upon me early in my studies, has been constantly in mind during the work. The facts are clear and abundant. They are capable of only a single interpretation so far as I can see. Under natural conditions the red salmon does return to spawn in the lake where it was hatched, but not because of that fact. The sequence has been reversed and what stands out as cause is really the effect. The fry follows a certain path to the sea because the adult female deposited her eggs in a certain gravel bed. The young salmon has no choice; it merely drifts down stream until it reaches the ocean.

One comes then to inquire what conditions determine the movements of the adult. To summarize briefly, I incline to believe that it attains a certain spawning ground because it is constrained by a series of circumstances, of environmental influences that hedge it about at all points in its migration, that compel it to follow one route and constrain it from leaving that pathway. About this migration there is much as yet unknown but nothing mystical; the story is marvelous but not inexplicable and its interpretation is to be sought and found in a thorough analysis of the multifarious and complex interacting factors of the environment. For a number of years I have been engaged in that work and believe I have made progress towards the solution of the question. Some of the results obtained may be considered next.

The Influence of the Stream Current

Among the environmental factors that influence the movement of the salmon no one would hesitate to include the current of the stream. The fish move steadily upstream, bucking the current. In studying the Columbia River salmon, Rutter (3: 122) made observations of great interest which illustrate the influence of current on the direction of movement.

In the lower reaches of the stream where tidal influences are felt, the salmon move upstream with the outgoing tide and later when the tide turns move downstream against its inflow. But, as the combination of tide and river current always produces an outflow longer and stronger than the inflow, so the upstream movement of the fish surpasses its briefer retrograde movement and the salmon passes sooner or later from the region of periodically reversing currents into that of constant outflow. Here its course is steadily upstream. Now while these observations were made on the king salmon, and have not been repeated on the sockeye so far as I know, yet probably the results apply equally to both species.

When a lake is included in the course of a stream the upward movement of the sockeye is halted for a time. The fishermen maintain that the fish rest in the deep waters of the lake and ripen before continuing their upward march. I have not had opportunity to observe carefully such a situation though I am familiar with the fact of the delay. It is evident that in a lake the current is very greatly reduced and may practically disappear so that the rheotropic stimulation is much reduced in intensity or perhaps entirely absent. In some short rivers in southeast Alaska I have noted that the salmon leave a lake at the time of a heavy rainfall and the sudden rise in water level accompanying it. That this is generally true I cannot say, neither have I any evidence to show whether, if so, it is due to the production of a current and a resulting stimulus, or to some other cause.

In the upstream movement of the sockeye there are two points where the current stimulus is not adequate to explain the movements of the fish. The first is the choice of a route at each stream junction and the second is the determination of a spawning ground. In both instances the fish do make a choice, and the selection is made promptly and definitely. These are crucial points in the fresh-water history of the adult salmon, and may properly be expected to show on careful study some evidence of the influences directing and controlling the movements of the fish. The two situations deserve consideration separately.

The Choice at Stream Junctions

I have already commented on the definiteness of the route which the sockeye follows in fresh water, and on the persistency with which it adheres to its age-long course. Now evidently every time a sockeye comes to a point where a tributary enters, it is offered an option; but with remarkable uniformity it selects one stream and refuses the other. Many persons have attempted to determine some difference in the water of the two streams which might enable the fish to discriminate between them. But heretofore the attempts have been unsuccessful and have only served to show that the sockeye is not influenced uniformly in its choice by the volume, depth, speed, or turbidity of the stream chosen in comparison with the branch which is rejected. An examination of some of the streams in southeastern Alaska showed very clearly that, although richly branched, many of these river systems cover so little total area that the different branches have substantially the same surroundings; they flow over identical rock formations, their banks are formed by the same sort of soil, they are fed by waters filtering through the same vegetation. Such uniformity in the environment postulates likeness in chemical constitution, and, even though no extensive chemical tests have been made, it is reasonable to hold that the branches of such systems at least do not differ in the chemical character of the water they contain.

After having studied various factors in the situation without having been able to detect any correspondence between them and the movements of the salmon, I turned my attention to one which so far as I know has not been tested by any other student of the problem. The factor in question is the temperature of the water. I was not at first deeply impressed by the differences which showed themselves between streams at junction points since they were in the main small, and since the fluctuations in the absolute level of the water temperature were in some cases great enough to confuse the situation in my mind. It was evident that different streams in the same general region varied considerably in actual temperature and that even in the same stream the water was noticeably warmer at one time than at another. Yet the fish moved upstream despite these fluctuations. As the evidence accumulated it became clear however that when differences in temperature between the two branches were present at the time that the fish were called upon to make the choice, the sockeye always chose the colder water.

I was led to the conclusion that the actual temperature did not affect the upstream movement, but that when a choice was offered the difference in temperature determined the selection of one stream above another. To avoid misunderstanding it should be stated that in my opinion temperature conditions do not constitute the only and all-powerful element in the situation. The reactions of animals are undoubtedly determined by a complex of factors and even though the temperature be significant, one can find circumstances under which its influence is not the controlling factor. I believe and purpose to show that, in many cases at least, its influence is decisive, and to leave for later discussion those instances in which other factors apparently reverse its action.

Within the natural limits of such a paper as this it is impracticable to give all the evidence collected in the study of such a problem or to discuss all of its aspects. It will be necessary to select a few typical instances and to indicate briefly their relations to the question. I have accordingly chosen to present the situation as I found it in my most recent field study made during the summer of 1919 on the Copper River in central Alaska. The data collected here were more extensive and more exact than those collected earlier; and it was of course possible to profit by the imperfections that became apparent in previous results.

OBSERVATIONS ON THE COPPER RIVER

The Copper River system furnished abundant opportunity to test the influence of temperature on the movements of the sockeye. It has a large number of branches which differ widely in source, character and temperature of water. It carries a big run of salmon which, within certain time limits, are almost all sockeyes.[2] The primeval conditions are hardly modified anywhere, and with rare exceptions the spawning grounds stand in natural form as they were when the region was an untouched wilderness. In an earlier paper (4, 119) I have described the river and its tributaries in general. Here it is necessary to discuss a few situations in greater detail in order to show more clearly the operation of the temperature factor in determining the movements of the salmon.

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[2] According to Bower (1) the total catch of the Copper River in 1918 was 50,189 coho, 20,849 king, and 1,588,838 red salmon. In 1919 it was 40,650 coho, 13,064 king, and 1,253,687 red salmon. Both years show that very nearly 96 percent of the catch is made up of red salmon.

The Copper River and Northwestern Railway runs close to the stream for a hundred miles up from its delta and made it feasible to examine rapidly that section of the river on the side of the valley traversed by the railroad. Fortunately the features of most significance for the problem under discussion are accessible directly from the track. I shall take them up in the order in which they are encountered in the work.

The river breaks through two ranges of mountains in its lower course, and there has no large tributaries but is fed by short turbulent streams. In the plateau that surrounds its upper course one finds longer side streams and large lakes. The delta crossed by the railroad is a complex of interlacing channels on a level plain. The water of the river is exceedingly turbid and often carries floating ice from the glaciers.

Among the different tributaries of the Copper River, the first visited was Clear Creek, a small stream that comes out of the mountains to the east of the valley and after a short course of less than five miles empties into the easternmost channel of the Copper, a few miles above the mouth of that stream. The railroad crosses Clear Creek on a trestle a short distance from its junction with the Copper. The water of the creek is perfectly clear, in contrast with the turbid opaque waters of the main river it joins here. The creek was examined very carefully from its junction with the Copper up to the point where it emerges from the narrow valley in the mountains on to the flat flood plain of the river. At the time of our first visit, July 22, the red salmon were schooling in considerable numbers in every pool along the course of the creek, and in some cases had already assumed the brilliant coloring of the ripe salmon.

There is no lake at any point along the part of the course that was visited. Near the mountains in a marshy stretch the stream is sluggish and spread out to several times its breadth lower down, but from the moment it leaves this area conditions are those of a winding stream with alternating deeper pools and shallow stretches of more rapid movement over a rocky and gravel bottom. Even in the pools, however, the current is distinctly felt and the fish must keep in constant movement to hold their position.

Not a single red salmon was seen above the point where the stream came from the broader, shallower and more sluggish area in the marshy region, and there was no trace of previous spawning in this territory. However, from a point a few yards below that area, throughout the more swiftly flowing section of the stream, salmon were abundant down to very near the junction with the Copper River where the waters were deeper and quieter. The bends of the creek were deeper, and the schools of fish larger in number, below the railroad trestle than in the stretch upstream from that point. There was also only scanty evidence of nest building in the lower section of the stream. From the trestle upstream in a somewhat broader channel than most of the course below, the nests were abundant (figure 1). Here and just above were the ripest fish at this date, and here the fish were spawning at a later visit, on September 6. There was, however, at that date no opportunity to examine the stream in detail.

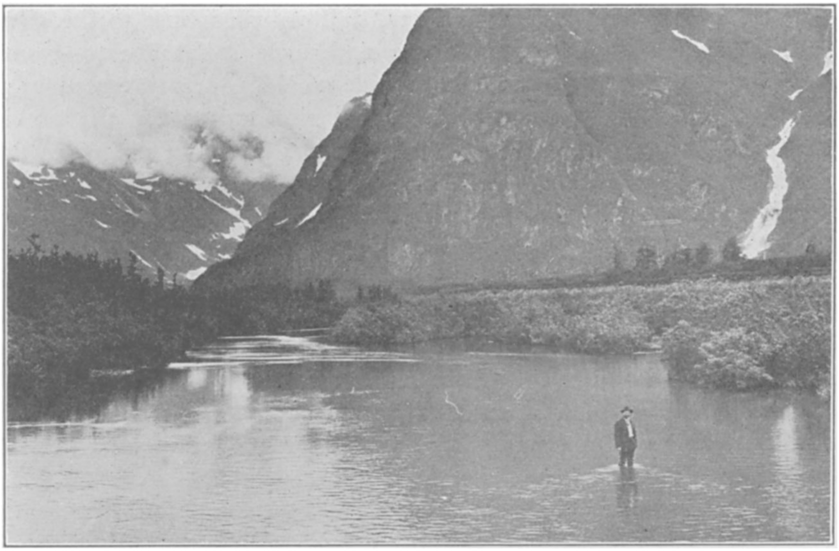

Fig. 1. Clear Creek from the railroad trestle. View upstream towards Goat Mountain. Salmon were spawning in this part of the stream, especially between the man and the bank on his left.

This shows clearly and strikingly how Clear Creek departs from the ordinary spawning ground of the red salmon.[3] Here the fish are spawning, not in or above a lake, but in a stream without a lake either above or below the spawning grounds. Furthermore, they have not picked out the more quiet or lake-like portion of the water-course but are found only in those parts which have a steady and considerable current. Finally, they have not penetrated to the real headwaters of the stream but are all grouped in the lower half of its course. No mechanical barrier stops them, any fish could easily go upstream some distance without encountering the slightest obstacle. Conditions of this type seemed to demand an inquiry into the exact conditions that prevailed. A series of temperature readings taken with some care showed the following situation:

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[3] "Red salmon streams without exception flow through lakes or have lakes tributary to them" (Jordan and Evermann, 2, 11).

The east channel of the Copper above the junction of Clear Creek had on July 22 at 11:30 A.M. a temperature of 48°.5 F. At the same hour the temperature of Clear Creek fifty yards above its mouth was only 44° F. At the trestle the temperature of the creek water was the same. Just below the marshy region it was again 44°, and the same temperature obtained through that region except that in a little spring-fed shallow extension at one side where were caught many red salmon fry, the temperature was 43°.5 F. The stream thus showed in the first place that it was, contrary to our expectations, 4° cooler than the water of the Copper River, and that at this time fish were coming into the creek. Yet occasional pieces of ice were floating into the Copper River, coming from the big glaciers at no great distance above this point.

It should be mentioned in this connection that the temperatures are not constant day by day, for on the following day, July 23, at 5 P.M., Clear Creek was about 2° colder, as the temperature at the trestle near the right bank was 42°, in the center 42°.5, and at the left bank 39°.5 F. On the same day the temperature of the Copper River where the track crossed the east channel of that stream stood at 49° F., indicating the same difference between the main stream and its tributary as found the day previous.

The salmon were confined to the lower section of Clear Creek. A more precise examination of the area just above the trestle was made by running a line of temperatures across the stream, from which it appeared that near the right bank the water was 43°.5 to 44° F., in the center full 44°, and near the left bank it varied from 41° to 42°.5 F. Furthermore, the lowest temperature indicated was found only over limited areas. The exact examination of these places demonstrated the presence of an inflow of seepage water not sufficient in amount to constitute a visible spring or localized at special points, but entering over a small area of the gravel bottom in sufficient quantity to reduce the temperature at that point very conspicuously below that of the rest of the stream.

The fish were most abundant and actively engaged in nest building, as well as furthest advanced in coloring, and consequently nearest the spawning period, in the section along the left bank supplied with the cold seepage water. Above the point where the stream emerges from the marshy region there was little or no cold seepage from the bank, and consequently the water was distinctly higher in temperature.

The amount of water added to Clear Creek by the seepage indicated must have been considerable, for the volume of the creek where it flows under the trestle is apparently at least twice as great as that carried when it emerges from the swamp area a mile or more above the trestle.

The case is especially significant because it represents conditions that contradict the accepted rule. There is no lake on the course which the red salmon follow, either above or below the point where they spawn. They have followed the pathway marked out by lower temperatures. These facts serve to illustrate, first, that the migrating sockeye enters the tributary carrying water lower in temperature than the stream in which it is moving; and secondly, that a lake in and of itself is not essential. In the large majority of cases, of course, a lake is present, and may easily be a factor in determining temperature conditions, thus being indirectly a controlling element in the movements of the salmon.

About 30 miles from the mouth of the Copper River two large ice streams, Childs Glacier and Miles Glacier, empty into the river nearly opposite each other on opposite banks of the stream. In front of one there is an expansion of the river of considerable extent, designated as Miles Lake. The entire north and east shores of the lake are formed by the glacier from which masses of ice are constantly breaking loose and floating away in the form of icebergs. This lake has long been recognized as a splendid fishing ground and all indications point to it as a resting place for the fish during their upstream migration. The fishermen maintain that the red salmon lie in the deeper waters and "mill around," or move slowly in circles around the lake passing over certain shoals and bars where the fishing is unusually successful. It would seem as if the waters of the lake should be distinctly colder than the upper portion of the stream, or indeed than almost any other part of the river; floating ice is abundant, and below the lake one constantly sees fragments of ice in the current. I secured certain readings which are significant in this connection. On July 23 the temperature of the left bank of the Copper just above the railroad bridge between the glaciers was about 47°.5 F. On the same afternoon the various channels of the Copper River further down varied from 46° to 49°. On July 21 the temperature of the water in the stream at the upper end of Abercrombie Rapids just above the lake was 51° F. Whether or not the fish really lingered in Miles Lake, as they stop in other lakes in the course of some streams which form the pathway of their migration, when they leave there is but a single option, namely, to follow the channel of the river up the rapids and on to the north. In this they are led by the current stimulus.

The volume of the river is large, and the fall within the short stretch just above Miles Lake known as the Abercrombie Rapids is sufficient to make this region a serious obstacle to the passage of the fish. They undoubtedly hang near the shore, taking advantage of every irregularity of the bank and moving from eddy to eddy. It is indeed impossible to believe that they should attempt to surmount the distance by going up in midstream, or where they would catch the full force of the current. For, while undoubtedly a dash would enable them to temporarily overcome the current, such a speed could be maintained only for a brief period, and the shores with their projecting boulders furnish the only resting place in the long descent of the waters. For this reason dip netting along shore has been extremely successful. The waters are so loaded with sediment that the sweep of the net is not seen by the fish as the dip netters, standing on improvised platforms, gather them in. That such dipping is done in the protected spots which serve as resting places for the fish is further evidenced by the fact that the fishermen recognize certain points as particularly advantageous for dip netting. They shift the positions of the platforms to conform with the changing stages of water and leave certain parts of the shore entirely free because offering less opportunity for taking fish. A single sweep of the net empties a pocket, and while the dip netter rests other fish dart in to fill the place and furnish material for his next effort.

The tributary streams on the west bank of the Copper River were examined and found at the time of our visit to be warmer than the main river. None of them carried any red salmon until Chitina Creek was reached. Here salmon were in the lake below the town, and spawning in the creek both in and above the town. The run was far advanced, as many fish had already been caught and dried for winter food. It was impossible to determine the relative temperature conditions at the time the sockeye entered the creek, and spawning had been evidently interfered with by the town so that inferences concerning natural conditions are hazardous. It should be recorded, however, that one favorite place for spawning was a large cold spring from which the owner had hard work to bar off the fish by a fence built to keep the place for private use. The way to a small lake higher up on the creek was closed by piles of brush and débris so that fish which might be seeking that naturally would be forced to spawn lower down. The interference here with natural conditions has been discussed more fully in another paper (4, 131). It should be remembered that the significant time for temperature studies is, of course, the period during which fish are entering the side stream. Later than that conditions may change. To determine the relative temperatures while the fish are in a stream spawning or ripening preparatory to spawning has little necessary bearing on the conditions that induced them to enter that particular stream.

Some evidence has been accumulated to show that in larger streams or lakes the salmon tend to follow the banks and that those moving along one shore form the basis of the run in the streams of that shore. This is not yet fully demonstrated and is only mentioned here as a possible element in the distribution to various spawning grounds of the fish entering the big lakes to which attention is next directed.

The Lakes and the Spawning Grounds

On the west side of the Copper River valley at a distance of 20 or 30 miles from the stream and about 150 miles from its mouth are three large lakes that have been said to be prominent spawning grounds for the red salmon. Lake Tonsina is the farthest south and the smallest. Lake Tazlina lies 50 miles northwest of it and is the largest. Lake Klutina located midway between is intermediate in size. The lakes are alike crescentic in form, surrounded, at least in part, by mountains and fed by the run-off of great glaciers. We visited only the two larger lakes. They are 20 to 30 miles long and 5 or 6 miles in maximum breadth. The upper horn of the crescent points nearly east and gives rise to a stream which is the outlet of the lake. The other horn runs nearly straight south into the mountains and is in connection with large glaciers. Each lake has several lateral tributaries. In each case we found that certain of these tributaries carried salmon and afforded spawning grounds for them, whereas others were without these fish. Conditions in certain of these streams which were visited fortunately at crucial times show the effects of temperature on the migration of the sockeye.

A considerable stream known as St. Anne Creek enters Klutina Lake from the northwest at about the center of the crescent. Two visits were made to this place, the first on August 10 while we were on our way up Lake Klutina and the second on August 19, on our return from the head of the lake. On August 10 the temperature of the lake below the mouth of the St. Anne Creek was between 49°.5 and 50° F. The temperature just above the mouth was 48°.5. In the creek some 200 yards from the outlet the thermometer registered the water temperature as 47° F. The lake is very shallow near the mouth of the stream, and the clear water brought by the creek can be followed some distance before it is lost to sight in the milky water of the lake itself. On proceeding up the creek we found large numbers of dead and spawned-out salmon lying on the bottom, lodged in the débris, and strewn over the banks immediately next the water's edge. Only a few live fish were still present in the stream. It was evident that the spawning period was practically finished. Abundant evidence could be seen to demonstrate that at relatively recent times nest building and spawning had utilized a large part of the bottom of the creek.

On our second visit to St. Anne Creek, August 19, it was apparent that the water level had fallen at least 12 to 15 inches. The dead fish had almost all disappeared, having been carried down by the water, or perhaps more largely eaten by bears, of whose presence the bank gave abundant evidence. Fish skeletons picked clean or only partly stripped, and heads or other recognizable fragments were found along the trails leading away from the water even up to a considerable distance from the bank of the stream. No dead fish were now floating in the creek, and it was only rarely that an occasional one was seen lying on the bottom. The low gravel stretches of the bank which a few days before had been covered with fish were now almost bare. The run was clearly at an end and the evidences of it were generally removed save that naturally one could recognize the nests on the bottom where the egg-masses had been deposited. On this day the temperature of the water was only 43° F. but its volume was so small that the influence on the lake was insignificant, since it spread over a large shoal and in the shallow water only 100 yards from the shore the thermometer recorded the temperature as 55° F.

The red salmon ascend this creek for some distance, abundant evidence of their spawning being obtained for three miles or more upstream from the outlet. At this point we deserted the water and did not return to it for several miles, above which point no evidence of their presence was detected, although there must be some small spawning beds because within 100 yards of the point where the creek emerges from St. Anne Lake we saw a few ripe red salmon hanging in the current of the stream. The lake itself is so shallow for half its extent next the outlet that one could touch bottom anywhere with a paddle. We hunted carefully along the shore both of this shallower portion and of the deeper half but found nowhere any trace of the red fish either living or dead, floating or lying on the bottom. Nowhere was there a sign in the shallow shore gravels or at the points where small streams and springs emptied into the lake that red salmon, or indeed any other species of that fish, had made nests during the present season or in a previous summer. I felt compelled accordingly to conclude that red salmon spawn abundantly in St. Anne Creek and in small numbers even ascend to its headwaters, but that they do not enter St. Anne Lake, or use its waters as a spawning ground, even though no mechanical obstacle stands in their way.

The water of the creek comes only in part from the lake, and the relative volumes evidently vary greatly at different seasons. On August 20 St. Anne Lake water was 55° F. and in the creek near its mouth the water had fallen to 43° F. Small cold brooks, springs and ground water of low temperature had been added to its volume in sufficient quantities to make the difference. The salmon had been spawning in the colder water of the creek; they had not come into the warmer water of the lake.

The influence of temperature is felt not only at stream junctions in directing the choice of the salmon, but also in leading them to select definite points for spawning. This has been shown in the cases of Clear Creek and St. Anne Creek already described, where the preference of the fish for colder water and spring-fed areas is certainly clear; but these are not the strongest evidence available, as was demonstrated by the more detailed study of extensive spawning regions.

The Precise Location of Spawning Beds

The selective effects of temperature are most strikingly illustrated in the region at the head of Lake Klutina (figure 2). We arrived there on August

11, and camped on the west bank, northwest of the mouth of the Hallett River, the first of the numerous streams which empty into the lake on that side. In a little bay between the camp and the mouth of the Hallett a small stretch of transparent water was seen near the beach, and off this point salmon were jumping frequently in the evening and again in the morning after our arrival. This clear water came from a small slough, in which we found half a dozen dead salmon and a few nests, though not much of the area had been utilized for spawning. The temperature of the water here was 38°.5 F., while along the shore outside the clear water it ran about 53°. Just outside the mouth of the slough, where the clear water mixed with the milky water of the lake, the surface was about 50° and the bottom temperature in water only some three feet away varied from 44° to 40°.5 at different places. The clear cold water, which was distinctly traced to numerous small springs in what was a general area of seepage, spread out over the bottom of the lake as it flowed out from the inlet and did not mix with the milky water of the surface. More than once where the water was stirred up we had a chance to look down through an eddy of clear water into the larger clear area which covered the bottom. Here the fish were

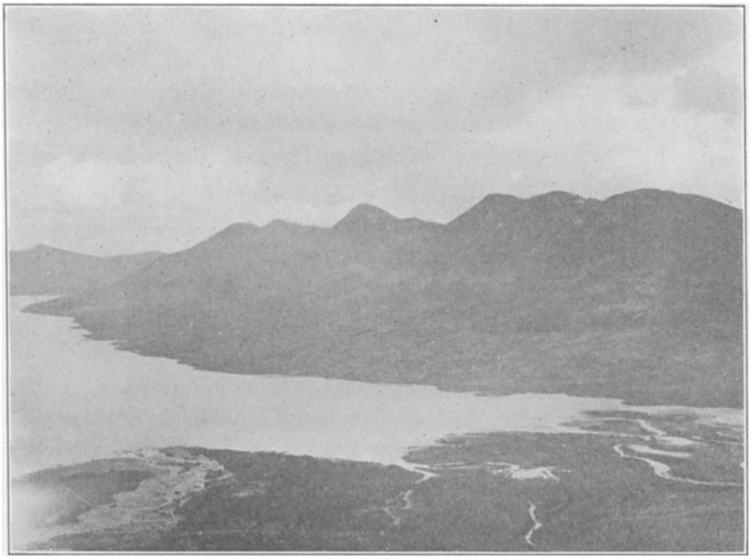

FIG. 2. Head of Lake Klutina, looking down the lake. The Hallett River enters at the extreme left, and the main (east) channel of the Upper Klutina River at the extreme right. Between are seen the inlets, sloughs, and subordinate channels mentioned in the text. The glaciers which feed the lake are separated from it by a valley of considerable length in which vegetation is old, and the blanket of muck is thick. From this area comes the flow of ground water which feeds the spawning beds of the salmon.

swimming about, marked by colors that indicated the near approach of the spawning time.

As we passed along this bluntly rounded end of the lake, we found that the lake water generally stood at from 49° to 50°. In the Hallett River itself, about a hundred yards up from the mouth, the thermometer registered 48°. The stream was shallow and rapid, and did not anywhere differ in temperature more than 0.5° from the record. We saw nothing to indicate that fish were entering the Hallett or had done so recently. Some time later we followed up this stream at various points to a distance of a mile or more from the mouth, without finding any evidence that it was or had been frequented by the salmon.

About 250 yards beyond the mouth of the Hallett was found another clear-water slough, in general appearance much like the one described above, although it was somewhat larger. It was followed up for a distance of one hundred yards or more. Near the mouth the temperature at the bottom in five feet of water was 39°. At the upper limit reached, where it was only 2 feet deep, the temperature at the bottom and the surface was alike 37°. In this slough there were a considerable number of living salmon in the bright colors of the spawning season, and some dead fish were also observed on the bottom. One could have found no more ideal spawning place. The bottom was good, the inlet well protected by old heavy timber on all shores. This inlet had no surface inflow, all of the water which came into it rising out of the ground and coming from general seepage or small springs, although the total amount received was sufficient to carry the clear water from the inlet well out into the milky waters of the lake. Fish were seen as far as the head of the inlet, and at least several hundred were swimming about in its waters. It maintained a uniform depth of about three feet for a long distance, and nests were abundantly distributed over the bottom of the entire area.

Another two hundred yards further on we found a minute inlet very similar in type. It was only fifteen feet wide, and varied in depth from two to four feet. Fifty yards would have measured the extreme length of the area. It had a good gravel bottom; but the inflow was imperceptible, and except from the clear water and the low temperature, which varied from 37°.5 to 38°, one would not have been able to distinguish it from the numerous other irregularities of the shore that were found all along the beach at this end of the lake. In this area there were 25 to 35 fish, including both dead and alive, and several nests.

The contrast between these clear-water sloughs just described and the milky-water regions similar in form and size which lay between and around them was very striking. Neither in shore material, in character of bottom, nor with reference to the amount and type of timber on the banks, the exposure to light or wind, nor in other mechanical features would one find the slightest difference. Yet certain of these indentations were filled with absolutely clear water of low temperature and the others were filled with the milky lake water that agreed in temperature with that at the surface of the main body of the lake. The clear water sloughs all sheltered red salmon, spawning or approaching the period of spawning activity, and all showed evidences that the salmon had been building nests on the bottom. In the indentations filled with milky waters not a single fish was seen, and the most careful search failed to give evidence of a single nest or other indication that the place had been visited by the red salmon.

This difference impressed me all the more forcibly in the case of one inlet having a common opening to the lake and several arms or branches, differing from each other in the following respects: The first arm, where the clear water began, was about 75 feet wide and from 3 to 5 feet deep, had a good gravel bottom which was well cleaned off, and a very gentle inflow over a small beaver dam. The temperature of the water was from 48°.5 to 49° F. The next branch, which was approximately the same size, had a temperature of from 50°.5 to 51°. The third branch was composed of muddy water, with a temperature that varied from 44°.5 to 45°. This branch proved on exploration to be the small westernmost channel of the Upper Klutina River which we later explored in considerable detail. Now the only fish that entered this group of branches followed up the colder one, which was filled with turbid water, rather than the warmer arms which were supplied with clear water.

Among the considerable number of other inlets and channels around the upper end of Lake Klutina were some much larger than those just described. In none of the blind inlets with warm water did we find red salmon spawning or any traces of their presence or previous activity. Those inlets which proved to be channels of the Upper Klutina were not investigated far enough to make positive statements concerning the presence or absence of fish in them. These river channels are cooler than the blind inlets which do not carry spawning salmon, and about equal in temperature to those clear water inlets where salmon were spawning.

To one who examined the waters the contrasts were striking. Some clear water inlets were selected by sockeye seeking spawning grounds, others were entirely rejected; some milky water areas were neglected, others were visited. The regions free from spawning fish were uniformly of higher temperatures and the places where the fish went, whether clear or milky, whether swift, slow flowing, or so nearly without current that none could be detected by ordinary observation, were one and all characterized by water temperatures that were distinctly low in comparison with the unfrequented waters. Finally, the precise points where nests were being made and eggs deposited were always in areas of seepage where ground water was escaping and the temperature was distinctly below that of the adjacent waters. In these cases no one could determine clearly that a current stimulus was not the determiningfactor, since in some cases the water flowed out in the form of numerous springs with evident vents where the disturbance of the gravel showed a considerable current, whereas in other instances the ground water exuded over a larger area and so slowly that a current could not be observed. All of the places where spawning was in progress had, however, a supply of ground water and as a natural consequence were characterized by low temperatures in the summer. This may certainly be assumed to be a natural condition, occurring as it does in the midst of a wilderness unmodified by any encroachments of civilization.

It is an immediate and unavoidable deduction from these observations that those regions where no reservoir of ground water exists and no spring-fed or seepage areas are to be found, will afford no proper spawning grounds for the salmon. Such regions were also present in the territory traversed (figure 3) and were easily recognized. The entire absence of salmon was noted in the field records while at the same time the general similarity of the area to that in which spawning had previously been observed was the subject of frequent comment by members of the party. The difference is

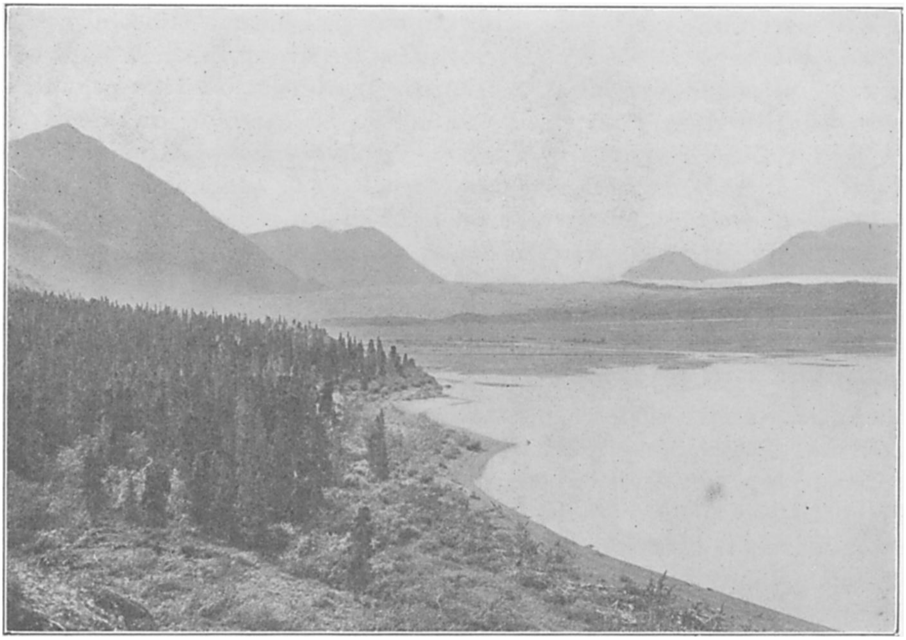

FIG. 3. Head of Lake Tazlina from a distance of a mile or more. Here the glacier is separated from the lake only by a narrow shifting zone of unstabilized morainal material. There are no fixed channels for the water, no trees or other vegetation, no muck layer, no spring-fed areas, and no spawning grounds for the salmon. Compare with figure 2.

fundamental although not apparent in the early study of the problem. But the fuller discussion of this aspect of the case may be left for another occasion.

TEMPERATURE STIMULI AND THE LIFE CYCLE

The factors which influenced the movements of salmon no doubt are numerous. It would be wrong to seek a single influence or expect to find one which will determine all of the movements of the fish. The theory that the adults go back to certain points because they were born there has been rejected. We must believe that a fish reaches a certain point because it is acted upon by external factors. Where there is a choice of streams, some physical factor determines that choice. So far as has yet been shown the temperature factor alone is definitely related to the choice of path. It appears that at the time the fish change their path, at the moment they come to a point demanding a choice, the stream which they choose is lower in temperature than the stream which they reject. Evidently in case both streams are alike in this respect, some other yet unrecognized factor may determine the choice.

The generally accepted view that the sockeye always selects a stream with a lake is certainly true in the main, even though I have described above in detail one instance in which no lake exists on the stream either above or below the spawning grounds. It is important to point out, however, that even when the lake is present, its relation to the spawning of the fish is rather variable. The fish may pass through two lakes and spawn in a third, as on the Naha River; they may pass through the first lake and spawn in a tributary stream on which there is another lake that they do not enter, as in St. Anne Creek with St. Anne Lake, described above; they may spawn in a tributary without another lake, like Salmon Creek, also on Lake Klutina; they may spawn in some part of the first lake reached, as in Baker Lake, or in Lake Klutina already discussed in this paper; or they may spawn in a stream above one and below two lakes, as in Chitina Creek, where alone of all the cases cited the evidence is not adequate to show that this is a natural relation. The evident variability of the relation between the lake and the spawning grounds of the sockeye, which could be further illustrated if need be, seems to me to be sufficient to show that such a water body is at most only indirectly essential when one considers the physical and climatic features in the regions in which salmon streams are located. I think it is likely that streams having a lake will be usually cooler than those without one. In the short warm summer, streams flowing over rocks and stones and broken up by rapids and falls will be warmed rapidly by air and sun, and a large reserve volume in a lake will tend to keep the temperature lower on branches connected therewith than it is on those branches that are without lakes. The actual volume of flow, the length of the stream, and the exposure of its waters will in individual cases modify this general relation. Now so far as my observations have extended, the movements of the sockeye accord with the temperature relations, and the lake is a somewhat variable associated factor. In exceptional cases, such as Clear Creek, they will select a stream without a lake. The selection in all cases I have tested is determined by the relative temperature of the waters at stream junctions.

The choice of a spawning ground is also of the utmost significance, and from the evidence presented seems to be determined by the temperature of the water. How very far-reaching this choice is becomes apparent when the further history of the eggs is considered. Various students of these fish have stated definitely that if the eggs are frozen[4] they will inevitably be destroyed, and on a priori grounds one would be forced to the same conclusion. The dangers of the situation are evidently ominous in the Copper River valley, for the soil is permanently frozen below the depth of a few feet, and a long rigorous winter sends the surface frost down in most places to join the frozen subsoil. Only where there is a stratum of uncongealed ground water moving slowly through the gravel and protected by the frozen muck above, could one hope to find the eggs escape the general congelation. The springs which in summer are coldest, will also be warmest in winter, or in other words furnish the most equable environment attainable. In confirmation of this view, I learned from officials of the railroad that Clear Creek in the stretch near the trestle keeps open long after other waters of the region are heavily frozen over. No doubt the considerable supply of ground water we demonstrated there keeps in movement under the ice even after the surface is well frozen.

On the other hand it seems clear that in the Copper River valley the amount of such spring-fed areas protected from freezing cannot be very large. In the upland on which are found Lakes Klutina, Tazlina, and others not visited but probably significant spawning grounds of the Copper River sockeyes, the climate is even more rigorous than at Clear Creek. Under such conditions the margin between life and death in the egg mass must be very narrow, and numbers are likely to perish in any year, while unfavorable variations in seasons will evidently destroy still greater numbers. This would easily account for marked fluctuations in the run and serve also to explain the disappointingly small number of salmon in the Yukon where conditions for spawning must be even more limited than in the Copper River basin. Such variations in the annual run of salmon have been recorded in several cases. One important instance is discussed by Bower (1: 31). The reason for these fluctuations has not been understood heretofore and some explanations given for it have certainly been inadequate. Under natural conditions the salmon run in streams of the far north is likely to fluctuate very widely from year to year. The situation becomes ominous when intensive fishing makes an added demand on the supply. The effect of such a combination will not be known until the year when the fish are due to return. In a given year the amount of ground water, the conditions of the streams in the summer, and the climatic conditions both in winter and summer will evidently exercise a great influence on the outcome of that year's spawning; and when several factors are unfavorable, the supply may be seriously affected in the season when the fish hatched in the unfavorable year return to spawn. Where the margin is so narrow in the struggle against an unfavorable, unyielding, and strictly limited environment, great variations in the yield must be expected. Under such conditions the preservation in unmodified form of the limited areas that are naturally favorable to reproduction is of supreme importance, for the species can not find substitutes. Evidently the sockeye, that perforce spawns outside the spring-fed areas which attract it naturally, will have no progeny, for its eggs will suffer total destruction in the winter freezing.

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[4] "Freezing kills the eggs" (Jordan and Evermann, 2: 5).

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